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**NOTES ON THE STUDY OF THE CROSS-FERTILIZATION OF FLOWERS
BY INSECTS.**

BY IDA A. KELLER.

One of the most remarkable discoveries in plant physiology was certainly that of the cross-fertilization of plants by the aid of insect visitors. That this discovery, made toward the end of the last century, was founded upon actual fact has been verified by almost every one who has become interested in this most remarkable phenomenon. Apparent as it is in many cases, in more instances, cross-fertilization by means of insects is simply a conjecture. There is no more fruitful source of error, perhaps, in the experience of all scientific knowledge than a sudden brilliant discovery, which is founded upon careful observations in a limited number of cases, and the wholesale application of its results without the exercise of sufficient caution. Again and again, the organic world has been shown to be so complex that no one simple formula can be found to express adequately the exact situation in each of a great variety of cases. Experience is constantly showing that each particular case must be carefully studied by itself before we can with any degree of certainty gain a thorough understanding of any general phenomenon in plant or animal life.

In my attempts to obtain an impartial view of the subject of cross-fertilization, so far as the actual observations made in this field up to the present day will permit, I was struck with a number of curious facts in connection with the development of our knowledge in this direction. I must, however, apologize for the rather meagre presentation of the subject. I have had neither the time nor the opportunity to acquaint myself thoroughly with its entire literature, and the original observations which I have made in this line are limited in number.

Conrad Sprengel, as we all know, discovered "The Secret of Nature Revealed in the Formation and Fertilization of Flowers." Over one hundred years have passed since this was recorded, and yet the plant world offers in this respect one puzzle after another.

Instead of having exhausted the study of the subject by this time, it seems to be gaining in interest.

Naturally enough, it was not the tendency of scientists to try to disprove what was evidently true from the observations of Sprengel, but rather to develop more fully our knowledge of cross-fertilization. I need only refer to the famous work of Darwin, to that of the well-known German botanists, Hildebrand, H. Müller, Kerner, and to that of the many close observers of our own day.

The fact that cross-fertilization is of utmost value to the individual species has been emphasized by Darwin. In fact, this great discoverer contends repeatedly that pollen applied to the pistil of the same flower is a positive injury to the species. It is curious to note how this idea has influenced the authors of botanical text-books. As one instance in many, I need only refer to Gray's *Structural Botany*. To the rather long chapter devoted to the description of the adaptation of flowers to insure intercrossing, a few paragraphs are added in which the writer, it seems to me rather unwillingly, admits that there are also special adaptations to insure close fertilization, in fact, that there are cases which positively exclude all chances of a cross. Of cleistogamous flowers, Gray says: "Here the intention and the accomplishment of self-fertilization are unmistakable. This peculiar dimorphism consists in the production of very small or inconspicuous and closed flowers, necessarily self-fertilized and fully fertile in addition to ordinary, conspicuous, and much less fertile, though perfect flowers."¹ He then continues: "It has been said that the ordinary flowers in such plants are sterile, and perhaps they always are so, except when cross-fertilized: in most cases they are habitually infertile or sparingly fertile. *Probably* they suffice to secure in every few generations such benefit as a cross may give, while the principal increase is by cleistogamous, self-fertilization, which thus offsets the incidental disadvantage of the former mode." I have quoted the writer verbatim, because the extract shows so plainly his mental attitude in regard to the significance of this phenomenon. Here we have a concession in regard to the extreme fertility of cleistogamous flowers, followed by a suggestion in regard to the few mostly infertile conspicuous flowers which accompany the former and from these, and the statement that

¹ Gray's *Structural Botany*, p. 241.

no species is altogether cleistogamous, taken as a premise, the following conclusion is drawn: "Thus, cleistogamy, with all its special advantage, testifies to the value of intercrossing." The same bias, looking favorably upon cross-fertilization, may be observed in most writers on the subject. The prevailing impression seems to be that close fertilization is, as a rule, only resorted to when all the chances for cross-fertilization are at an end.

It appears that the problem permits of a wholly different solution. Among the few writers who admit this, there is perhaps none who speaks with as much decision and who adduces as many facts to prove his assertions as does Mr. Meehan. In his interesting paper, entitled "Are Insects any Material Aid to Plants in Fertilization"—the conclusions are as follows:—

First: The great bulk of colored flowering plants are self-fertilizers.

Secondly: Only to a limited extent do insects aid fertilization.

Thirdly: Self-fertilizers are every way as healthy and vigorous, and immensely more productive than those dependent on insect aid.

Fourthly: That where plants are so dependent, they are the worse fitted to engage in the struggle for life, the great underlying principle in natural selection.

These views are directly opposed to the impression one would naturally receive from text-books on botany. It is evident that it is of the utmost importance to study the significance and, if possible, the cause of each of the various factors with which we have to deal as pointing either towards cross- or towards close-fertilization. As already suggested, it is always a critical matter to generalize where thousands of species are concerned which have developed under a variety of circumstances.

Let us now consider the chief adaptations which point towards cross-fertilization:—

- I. Distinct sexes.
- II. Specially adapted or conspicuous corolla.
- III. Peculiar position of stamens and pistils.
- IV. Difference in the time of maturity of stamens and pistils.

I. *Distinct sexes.* The male and female flowers being separated it is a matter of necessity that the pollen of one flower finds its way to the stigma of another flower. From a teleological point of view

the intention is clearly shown. We cannot, however, speak with certainty of cross-fertilization even in all these cases, except in wholly dioecious plants, at least not in Darwin's understanding of the term, which is, that "cross-fertilization always means a cross between distinct plants raised from seeds." We must, therefore, be careful not to include too hastily in this category monoecious plants, where the male and female organs are borne on distinct flowers but on the *same plant*.

II. *A specially adapted or conspicuous corolla.* It is these showy, irregular or peculiarly shaped corollas that insects may readily be observed to visit. The questions which here arise are numerous. The first one to present itself is this: Has the corolla been developed for the purpose of attracting insects, and is it the proof which nature gives us that cross-fertilization is a necessity or that it is at least favorable to the preservation of the species? This seems to have been definitely answered in the affirmative. The number of cases where the insect has actually been seen to transport the pollen from one plant to another, however, are few, compared with the great number of species whose flowers would come under this head. In this connection it must be remembered how very often the insect is simply a robber. This past summer I observed, *e. g.*, a very large patch of *Gerardia pedicularia*, the flowers almost all being pierced at the base of the corolla by bees perching on the outside and never touching stamens or pistil. Now, wherever it is more convenient for the insect to reach the desired substance without boring a hole it is apt to be taken for a benefactor, even if it simply takes from the flower without rendering any service in return. There is another suggestion I would offer in regard to insect visitors. In observing bees travelling to and from flowers of *Kalmia latifolia* I noticed that very frequently pollen is thrown upon the pistil of the same flower when the stamens are unfastened by the insect. I am not prepared to assert, however, that such flowers proved fertile. I simply throw this out as a suggestion and it should be taken for what it is worth. Professor Willis made somewhat similar observations on the flowers of *Phacelia tanacetifolia*. He describes the crawling of insects over the dense cymes; touching stamens and styles indiscriminately, and probably knocking the pollen on the stigmas from the surrounding anthers.² Further, he says in regard to *Phacelia Campanularia*:

² Contributions to the Natural History of the Flower, Jour. Linnaen Society, London, Botany, Vol. XXX, p. 55.

“Bees alight sometimes on the corolla, touching styles and stamens, crushing them all up together with the styles, and probably causing self as much as cross-fertilization.”³ This in spite of the fact that the flower of this plant is to all appearance well adapted to secure cross-fertilization. I should not be surprised if, sooner or later, upon close examination, it would be found that in many cases where this adaptation to insects seems so perfect, the insect visitors aid in securing self-fertilization, as these observations seem to indicate.

III. *Peculiar position of stamens and pistils.* In the preceding paragraph I have already briefly referred to the flowers of *Kalmia latifolia*, perhaps the best illustration of such an arrangement. The wheel-shaped corolla, with the ten pockets in which the anthers are held, is sufficiently familiar to require no further description. Stamens and pistil mature at the same time. The anthers are held in the pockets of the corolla; when visited by insects they are set free and the pollen is thrown with considerable force from the anther sacs through the orifices. As I have remarked before I have observed repeatedly that pollen was thrown upon the stigma of the same flower. Careful observations should decide the question, how far in such cases, where there is such a peculiar arrangement in the position of stamens and pistils in regard to each other, close fertilization is possible.

Even should it be impossible in any case that autogamy, or close fertilization, is effected, it must be remembered that whenever a plant bears many, or clusters of flowers, the chances of cross-fertilization are reduced. Insects in such cases may visit many flowers of the same plant, but this is not cross-fertilization in Darwin's sense of the term.

IV. *Dichogamy or difference in the time of maturity of stamens and pistils.* This appears to me the most suggestive and interesting phase of this intricate problem. From a teleological point of view, *i. e.*, if we look for a purpose, we must agree with Darwin and his followers that this is one of the most remarkable adaptations favoring cross-fertilization. Modern science insists, however, that we must use inductive methods, and it is the tendency of the present day to search rather for the causes than for an underlying purpose. If, on the one hand, we affirm that every organ is modified to serve some particular use, we cannot believe, on the other hand, that such modifi-

³ Ibid., p. 57.

cations are directly due to external factors over which the plant has no control. I am aware that the principle of natural selection may find its application in the most subtle cases; at the same time it requires, in this particular instance, a considerable strain to make it fit. In reference to dichogamy Mr. Meehan says positively that the difference between the time of maturity of stamen and pistil is caused by varying degrees of temperature and that dichogamy has its origin in this circumstance, "that whatever its significance, it arises from no effort innate to the plant itself, but from an outside force that can have but little interest in cross-fertilization."⁴ It is peculiarly characteristic of the present day to seek for the effect of external conditions and to experiment with the modifications that can be brought about by changing these. For example, Prof. Goebel says in reference to cleistogamic flowers, "We do not yet know the conditions necessary for the production of cleistogamic flowers, but it may be assumed even now that this production is influenced by external factors wherever a plant has the power to produce such flowers."⁵ He then cites experiments made with *Impatiens fulva*, where cleistogamic flowers are the result of poor nutrition. Accordingly, it appears at least possible that experiments might give similar results in reference to dichogamy.

Attention has often been called to the fact that in plants especially adapted to insure cross-fertilization, there exists in almost every case a possibility of self-fertilization. The above statements in regard to dichogamy, if of any value, point to a different conclusion concerning the final or at least possible autogamy from that which is generally accepted. It is assumed that the flower is so constructed that there is every chance of a cross, provided the insect appears to do the work. This failing, the arrangement is such as to allow pollen to come in contact with the stigma of the same flower. It is evident that in every case which seems to point towards cross-fertilization it is always to a great extent a matter of chance whether the visitor arrives or not, even when the adaptation seems most perfect. It should be decided if cross-fertilization or autogamy is the rule with every species which seems constructed so as to attract insects, and this work should be done in as many different

⁴ Proc. Acad. Nat. Sci. Phila., Nov. 27th, 1888, p. 394.

⁵ Goebel, Pflanzen-biologische Schilderungen. Marburg, 1893, II Theil, 2 Lief., p. 363.

localities and at different times of the year as possible, since there is no doubt there are great variations possible in the fertilization of flowers in the same species caused by different conditions of heat, moisture, etc.

If autogamy should in any case prove the rule we must regard fertilization by aid of an insect as an exception, not to call it an accident. Dichogamy probably is then in a measure due to external conditions. If this is true it is simply the result of a "lagging behind" in the ripening time of either stamens or pistils, and the final autogamy is the result of a subsequent "catching-up" in this respect. This is, as I have said before, probably the most interesting side of the question, and the one which will no doubt prove the most satisfactory for experimental investigation.

In conclusion I desire to make the following suggestions:—

First:—It is evident that the study of the phenomenon of cross-fertilization of flowers by means of insects is still a profitable field for observation and discovery.

Second:—The effect of external conditions in reference to dichogamy should be the subject of critical experiments.

Third:—Teleological explanations should be avoided as much as possible, here as elsewhere, according to the spirit of modern investigation.

Finally:—The relative number of cases of cross- and close-fertilization should be compared, and it should be determined if cross-fertilization actually takes place in all cases where this is assumed.